However, there are still many questions to be answered in the aetiology and pathogenesis of the nutritional myopathy of the quokka and in muscular dystrophy. Useful comparisons of the muscle lesions in the two conditions have been in terms of the common principles which are responsible for the histopathogenesis of the respective myopathies and it is probable that necrosis in both is due to a basic membrane defect. However, apart from this, very little has been gained from the quokka investigation which has shed light upon the aetiology of muscular dystrophy. Vitamin E as an anti-oxidant is known to prevent the peroxidation of membrane lipids and there is evidence that the human dystrophies, especially dystrophia myotonica, are also basically due to membrane disorders (Rowland 1976). This common ground between the animal and human myopathies deserves further exploration.

The quokka myopathy is primarily due to nutritional deficiency of vitamin E, while human muscular dystrophy is genetically determined. However, this does not preclude the possibility that both conditions act within the same biochemical pathway, i.e. the metabolic disorder in the animal is an "acquired" defect of the system, which is responsible for the maintenance of membrane integrity, and that the biochemical disturbance in man is a hereditary "inborn error" of membrane metabolism. The naturally-occurring myopathy of the quokka is clinically, a more acute disorder than the Duchenne and other forms of human muscular dystrophies, otherwise their pathological manifestations are remarkably similar.

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Recent endocrinological research on the Rottnest Island quokka

(*Setonix brachyurus*)

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Abstract

Recent endocrinological work on the macropodid marsupial, the quokka, (*Setonix brachyurus*) is reviewed. concentrating on pituitary, adrenal and reproductive hormones. Studies of adeno- and neurohypophysial hormones are in their infancy and the significance of the suite of newly-discovered hormones in the pars nervosa needs to be established. Recent research on circulating levels of progesterone in the quokka have shown that the oestrous cycle and the pregnant cycle are not hormonally equivalent, as was previously thought. The chorio-vitelline placenta of the quokka has also been shown to be capable of progesterone synthesis *in vitro* and there is mounting evidence in this species, and in other marsupials, that the conceptus exerts a strong local effect on the uterus.

Introduction

Despite the fact that the quokka is a member of a monotypic genus restricted virtually to insular habitats in Western Australia, it has proven a particular accommodating vehicle for a wide variety of research, due primary to its ready availability and ease of maintenance in the laboratory. Such is the extent of this work since the last major review of the animal's biology in 1959, that this report will be concerned only with pituitary, adrenal and reproductive hormones. Research on the thymus gland and immunology is reviewed by Stanley (this volume) and the ecological relevance of much of these data is discussed by Main (this volume). McDonald (1977) has recently reviewed what little

is known of adrenocortical function in marsupials and McDonald and Waring (1979) combined to produce a major review of hormones and their effects in marsupials and monotremes. For a broad and succint overview of the physiology of the quokka however, the reader is referred to Waring *et al.* (1966) which still remains current as one of the best reviews of the comparative physiology of marsupials.

Pituitary function

Traditionally, pituitary function is assessed following surgical hypophysectomy but this has never been reported in the quokka, only in the closely-related tammar wallaby, *Macropus eugenii* (Hearn 1975). The cytology of the quokka pituitary was described by Wingstrand (1966) and the neurohypophysial peptides tentatively identified as arginine vasopressin and oxytocin (Ferguson and Heller 1965, Acher 1974). Bakker and Bradshaw (1978) developed a sensitive bioassay for the measurement of circulating levels of antidiuretic hormone in the tammar and the quokka but recent studies from Acher's laboratory have revolutionised our knowledge of marsupial neurohypophysial hormones.

Acher and his colleagues in Paris, using separation and detection methods with greatly heightened sensitivity, have shown that the major neurohypophysial hormone in the quokka is not arginine vasopressin, but lysine vasopressin, a rare hormone thought previously to occur only in members of the pig family (Suina) and Peru strain mice (see Acher *et al.* 1981). A second novel peptide was also identified as phenypressin (Phe^2-Arg^8-vasopressin) (see Chauvet *et al.* 1980) and, even more surprising, was their discovery that the oxytocic principle of the quokka pituitary is not oxytocin, as in other mammals, but mesocotin (Ile^8-oxytocin). previously thought to occur only in lower vertebrates (Chauvet *et al.* 1981). The structure of these novel hormones is given in Table 1 from which it may be seen that they differ only by single amino-acid substitutions in the 2, 3 and 8 positions. Acher's work has also shown that the quokka is by no means unique amongst marsupials in its possession of such a constellation of peptides in the pars nervosa and there is evidence that phenypressin occurs as well in *Didelphis*, the North-American opossum.

The significance of these findings is difficult to assess at this stage as nothing is known of the physiology of these hormones. As Bakker and Waring (1976) were able to induce diabetes insipidus in the tammar by the placement of electrolytic lesions in the base of the hypothalamus, clearly one of these peptides must function as an antiduretic hormone, and one would opt for lysine vasopressin which is slightly less active than arginine vasopressin in eutherian mammals. Similarly, mesotocin presumaly functions as the galactogenic hormone in marsupials but the rôle of phenypressin is obscure. More research in this area is imperative, especially as early work by Acher *et al.* (1973) established that the prototherian echidna (*Tachyglossus aculeatus*) has arginine vasopressin and oxytocin in its pituitary and thus does not differ from the conventional eutherian pattern.

Very little is known of the nature and structure of the adenohypophysial hormones of the quokka, or of any other marsupial for that matter. Farmer and Papkoff (1974) reported the presence, in whole pituitary glands from the red kangaroo, of separate fractions with chemical properties similar to eutherian luteinizing hormone (LH), follicle-stimulating hormone (FSH), prolactin and growth hormone. Bona Gallo *et al.* (1978) reported further fractionation of pituitary gonadotrophins from tammar pituitaries and further studies on marsupial adenohypophysial hormones were reported recently by Farmer *et al.* (1981).

Adrenal hormones

Ilett (1969) first reported the presence of cortisol and corticosterone in adrenal venous and heart blood of the quokka, and he noted that they were in roughly equal concentrations. Oddie *et al.* (1976) subsequently reported a cortisol : corticosterone ratio in the peripheral blood of the quokka of 2.03 which probably indicates that sample collection was attended by some stress. McDonald and Bradshaw (1977) again found roughly equal concentrations of cortisol and corticosterone in the plasma of unstressed quokkas but, with stress, cortisol levels rose disproportionately to reach a ratio of 2.59.

McDonald and Bradshaw (1977) used indwelling jugular catheters to obtain blood samples from un-

Table 1

Amino-acid sequences of arginine, lysine vasopressin and phenypressin, oxytocin and mesotocin

Peptide	Amino-acid sequence	Distribution
Phenypressin	1 2 3 4 5 6 7 8 9 CYS - *PHE* - PHE - GLN - ASN - CYS - PRO - ARG - GLY - (NH$_2$)	Red kangaroo, tammar plus (?) quokka. grey kangaroo, euro and *Didelphis*
Arginine Vasopressin	CYS - TYR^2 - PHE - GLN - ASN - CYS - PRO - ARG - GLY - (NH$_2$)	Eutherian mammals plus echidna
Lysine Vasopressin	CYS - TYR - PHE - GLN - ASN - CYS - PRO - *LYS*^{8} - GLY - (NH$_2$)	Pig, warthog, peccary, hippopotamus, Peru strain of mice, red kangaroo, grey kangaroo, euro and (?) quokka and tammar
Oxytocin	CYS - TYR - ILE^3 - GLN - ASN - CYS - PRO - *LEU*^{8} - GLY - (NH$_2$)	Eutherian mammals plus echidna
Mesotocin	CYS - TYR - ILE - GLN - ASN - CYS - PRO - *ILE*^{8} - GLY - (NH$_2$)	Quokka, red kangaroo, euro, tammar and possum

restrained animals and repeated sampling at three-hourly intervals over a period of two days failed to disclose any evidence of a diurnal cycle in cortico-steroid levels. Irregular fluctuations occurred over the range of 0.4-5.0 μg/dl but there was no evidence of a regular periodicity. Similarly, short-term sampling at five-minute intervals, gave no evidence of episodic secretion by the adrenals. Con-stant-rate intravenous infusion of either porcine adrenocorticoptrophic hormone (ACTH) or syn-thetic β^{1-24} ACTH caused a significant increase in the concentration of total corticosteroids in the plasma, being detectable at a dosage of 0.05 i.u./kg/hr and rising to approximately 15 times the control value at a dosage of 2.0 i.u./kg/hr. This increase in the rate of adrenal corticosteroidogenesis was log-dose related and both porcine and synthetic ACTH were found to be equipotent. This increase in circulating steroid levels was due almost exclusively to increased secretion of cortisol and levels of corticosterone and the minor component, 11-deoxycortisol, remain vir-tually unchanged.

Herrick (1961) was the first to attempt some assessment of adrenal function in quokkas on Rott-nest Island and relate this to seasonal changes in condition of field animals. The techniques available at this time however did not permit measurement of circulating corticosteroid concentrations and adrenal ascorbic acid levels were used as an index of secretory activity. He found that dehydration was associated with depletion of adrenal ascorbic acid levels but, contrary to expectations, quokkas collected from "dry" areas of Rottnest in the summer 1958 did not have significantly lower ascorbic acid levels than those maintained on adequate supplies of food and water in the yards.

The development by Bakker and Main (1980) of a Condition Index based upon the regression of the length of the tibia on the cube root of the body weight has considerably simplified the assessment of seasonal changes in physiological condition. Miller and Bradshaw (1979) employed the Condition Index to follow seasonal changes in a discrete population of quokkas on Rottnest Island, localised just West of Green Island. Whereas previous reports have emphasized the dramatic loss of condition of the quokka over the summer season (e.g. Barker 1974; Barker et al. 1974. Main 1970), Miller and Brad-shaw (1979) found that animals were in significantly better condition during the hot-dry period (Nov-ember-March) than in the cool-wet season (April-October) (Condition Index of 6.3 ± 0.19* versus 5.3 ± 0.15, p < 0.001). Plasma corticosteroid levels were also significantly higher in the cool-wet season, indicative of greater environmental stress, and the total body water content was increased, indicating poorer condition. These changes are plotted season-anlly in Figure 1 from which it is clear that the quokka experiences a progressive decline in body condition from a peak in about November; and mid-winter, rather than mid-summer, is the most difficult period physiologically. Plasma corticosteroid con-centrations were negatively correlated with the Con-dition Index (r = -0.85, p < 0.01) indicating the in-cidence of adrenal-mediated stress in a natural population of marsupials.

Aldosterone concentrations in the peripheral cir-culation of the quokka of 6.6 ± 3.4 ng/dl were reported by Oddie et al. (1976) and Miller and Bradshaw (1979) recorded on overall mean of 7.78 ± 0.40 ng/dl from their field study. They also found that aldosterone concentrations did not differ on Rottnest between the hot-dry and cool-wet sea-sons, but that there was a marked fall to levels of about 4 ng/dl in mid-winter. Laboratory experi-ments by these authors with quokkas maintained on high and low-salt diets showed that plasma aldo-sterone levels are very sensitive to changes in sodium status, falling from a mean of 16.95 ng/dl on the low salt diet to a mean of 2.33 ± 0.57 ng/dl on the salt-replete régime. These figures suggest that quokkas on Rottnest experience an adequate sodium intake for the majority of the year but may experi-ence a surfeit in mid-winter.
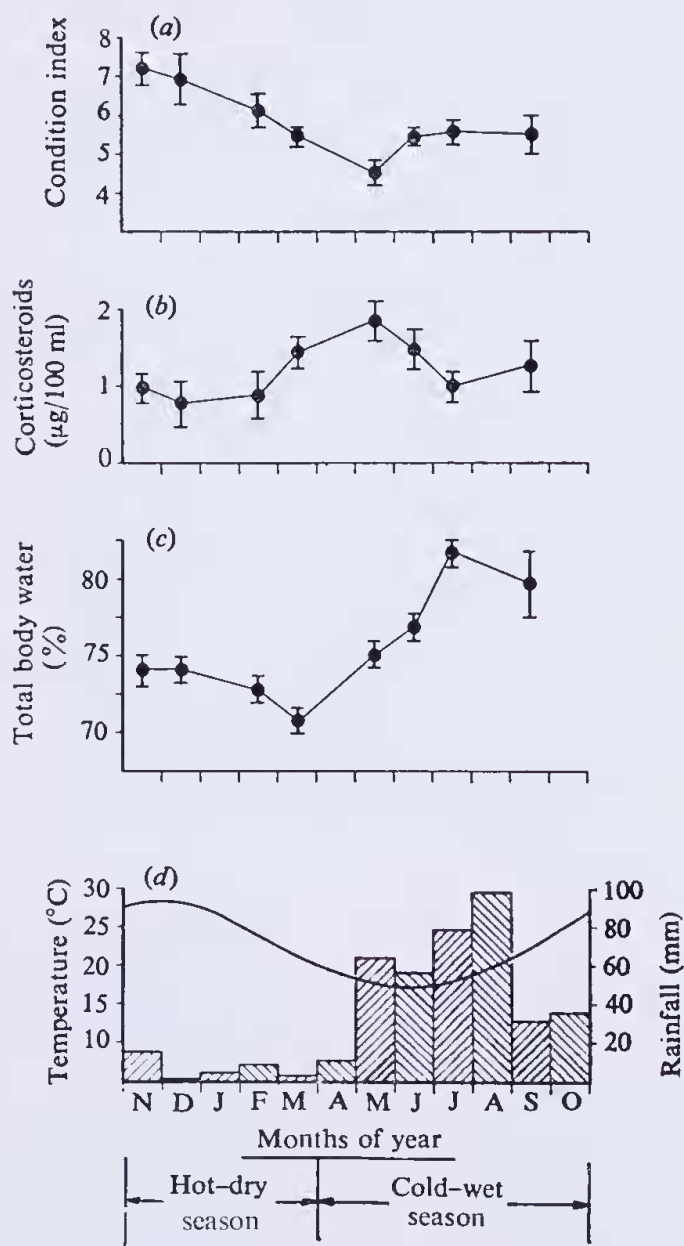

Figure 1.—Seasonal changes in the Condition Index, Plasma corticosteroid concentrations and total body water content in the quokka (Setonix brachyurus) on Rottnest Island. (From Miller and Bradshaw 1979, with permission).

*All values in text presented Mean ± S.E.

Dramatic confirmation of this comes from the study of Miller and Bradshaw (1979) who measured circulating levels of aldosterone in "coastal" and "inland" quokkas and found a highly significant difference, with the level of aldosterone in the plasma of "coastal" animals being almost half that of "inland" individuals and the urine was significantly more concentrated in sodium. Subsequent unpublished work has confirmed, with the use of salt traps that winter storms deposit large quantities of salt on the vegetation on Rottnest (see Ambrose *et al.* 1980) which is then ingested and subsequently excreted by the quokkas.

One striking aspect of adrenal function which deserves mention is the apparent lack of a diabetogenic action of steroids such as cortisol in the quokka and some other marsupials. McDonald and Bradshaw (1981) found that injections of cortisol at dosages of from 1 to 5 mg/kg per day were without appreciable effect on urea nitrogen excretion and did not elevate blood glucose levels. One of the major actions of glucocorticoids in eutherian mammals is to enhance catabolism of muscle and hence urea excretion (thus "diabetogenic" action). This refractoriness to the nitrogen-mobilizing action of cortisol does not appear to be a marsupial characteristic however, since Than & McDonald (1974) found the brush-tailed possum to be quite conventional in this respect.

These data force one to reconsider the metabolic role of glucocorticoids in such marsupials as the nitrogen-mobilizing effect is thought to be fundamental to the metabolic action of glucocorticoids in mammals (see Munck 1971). Bradshaw and McDonald (unpublished) have recently examined renal function in adrenalectomised quokkas in an effort to identify the rôle of adrenal corticosteroids such as cortisol and aldosterone. Glomerular filtration rate (GFR) and renal plasma flow were measured simultaneously in conscious unrestrained animals by clearance of ^{14}C-inulin and ^{3}H-PAH as detailed by Bakker and Bradshaw (1983) working with the hare wallaby, *Lagorchestes conspicillatus.*

Adrenalectomised animals were maintained post-operatively on a daily régime of 0.2 mg/kg cortisol plus 10 μg/kg aldosterone injected intra-muscularly This régime seemed adequate to maintain the animals in good health indefinitely, but interesting differences were noted in renal function when compared with intact individuals. The clearance of PAH for example was reduced in the operated animals on maintenance therapy (from 15.1 to 10.3 ml (kg.hr)$^{-1}$) and the filtration fraction increased from 27% to 38%. It is apparent therefore that, despite a fall in renal blood flow consequent upon surgery, glomerular filtration was still maintained, apparently by autoregulation. Withdrawal of the maintenance régime for a period of from 48-72 hours resulted in
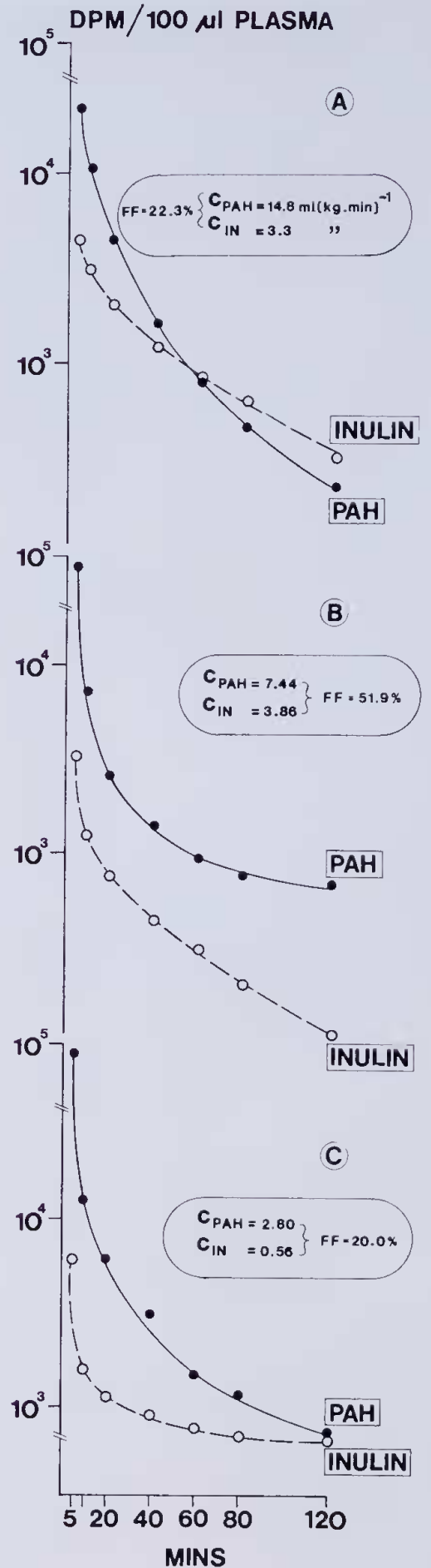

Figure 2.—Disappearance curves for 14C-inulin and 3H-para-amino-hippuric acid (PAH) following a single intravenous injection in the quokka (*Setonix brachyurus*). The injection was given at time zero and samples taken subsequently at times 5, 10, 20 etc., mins. A = intact individuals; B = bilaterally-adrenalectomised animals on maintenance régime of 0.2 mg/kg cortisol plus 10μ g/kg aldosterone per day; C = bilaterally-adrenalectomised animals 48-72 hours after withdrawal of maintenance régime. (From Bradshaw and McDonald, unpublished).

Table 2

Clearance of inulin (C_{IN}), para-amino hippuric acid (C_{PAH}), rate of urine production (V) and the filtration fraction (FF) in intact and adrenalectomised quokkas and the effect of steroid maintenance therapy. (Data as means $\pm$ S.E.). From Bradshaw & McDonald (unpublished).

Treatment (N = 6)	V	C_{IN} ml (kg.min)$^{-1}$	C_{PAH}	FF %
Intact	0·021 ±0·003	3·71 ±0·38	15·07 ±2·35	26·9 ±4·7
Adrenalectomised +Maintenance Régime*	0·073 ±0·022	3·50 ±0·20 p0·05	10·30 ±2·24	38·1 ±4·2
Adrenalectomised	0·026 ±0·008	<1·47 ±0·59	5·02 ±1·93	23·0 ±5·8
Adrenalectomised +Aldosterone ...	0·048 ±0·002	3·11 ±0·10	7·98 ±1·23	40·4 ±4·7

* 0·2 mg(kg.day)$^{-1}$ cortisol ÷ 10 μg(kg.day)$^{-1}$ aldosterone.

p<0·05 compared with intact animals.

a rapid decline in the condition of the animals and both the GFR and the PAH clearance fell markedly under these circumstances. Representative clearance curves for both PAH and inulin from intact and adrenalectomised quokkas with and without maintenance therapy are shown in Figure 2 and the virtual complete renal failure in the absence of steroid injections is quite evident. In those animals which did die, the classical symptoms of anorexia, muscular weakness and listlessness were evident and death resulted from circulatory collapse. Renal parameters from intact and adrenalectomised animals are summarised in Table II.

Reproductive hormones

The control of reproduction in macropodid marsupials was reviewed by Tyndale-Biscoe et al. in 1974 but is it important to note that only the most preliminary of hormonal data were available at the time. Influential reviews of reproductive physiology of marsupials such as that of Sharman (1970) have thus not benefited from an extensive literature on circulating hormone levels as is the case with eutherian mammals and, as more of this information becomes available, it is forcing a revision of earlier standpoints. Primary amongst these is the assertion that the pregnant and non-pregnant states are endocrinologically equivalent in marsupials. In the eutherian mammal of course pregnancy is "recognised" by the mother on implantation of the blastocyst by the failure of the corpus lutem to degenerate. Hormonal differences are also evident from an early stage, emanating both from the conceptus and the altered maternal physiology. In the latter stages of pregnancy in eutherians, the placenta as a potent progesterone-secreting endocrine organ, dominates gestation.

The marsupial situation is of course very different from this. Pregnancy per se does not inhibit ovulation and gestation is contained within the length of a single oestrous cycle. Birth can occur at any stage throughout the cycle and the uteri from pregnant and non-pregnant animals appear identical histologically. Blastocysts have also been transferred

successfully and developed to term in the uteri of virgin recipients and it is not perhaps surprising that the idea of hormonal equivalence gained sway. Recent studies with the quokka and other species however have forced a reappraisal of this position.

Poole (1975) noted, in hybridization experiments between eastern and western grey kangaroos, that the length of the gestation period is determined by the genotype of the foetus rather than that of the mother. Renfree (1972) found that there is a significant local effect of the conceptus in the pregnant horn in the tammar which possesses a hypertrophic endometrium when compared with the contralateral horn. More significantly, the pregnant horn secretes a specific β-globulin not present in the non-pregnant horn, thus establishing a local effect of the conceptus. Heller (1973) was sceptical of the claims that the placenta is not an endocrine organ in the marsupial and studied the pharmacological effects of oxytocin and vasopressin on the contractility of the quokka uterus during pregnancy and the oestrous cycle. He found the response of the pregnant uterus to be always greater to oxytocin than to vasopressin whereas the reverse was true in non-pregnant animals. Differences were also observed in the reactivity of the endometrium during the follicular and luteal phases of the oestrous cycle which were indicative of an effect of progesterone. Following on from this study, Bradshaw, et al. (1975) reported that the chorio-vitelline placenta of the quokka was capable of transforming the steroid precursor pregnenalone into progesterone in vitro, thus establishing its steroidogenic capability. Heap, et al. (1980) subsequently confirmed that the placenta of the tammar is also capable of progesterone synthesis.

The first clear evidence of an hormonal difference between pregnant and non-pregnant marsupials comes, however, from a recent study of plasma progesterone levels in the quokka. Cake et al. (1980) developed a highly specific and sensitive radio-immunoassay for the measurement of peripheral progesterone concentrations and employed the technique of indwelling chronic jugular catheterisation to obtain daily blood samples from unrestrained and unstressed animals. Daily mean plasma progesterone concentrations in three pregnant and three non-pregnant quokkas are shown in Figure 3 and the spike on day 3 in the pregnant cycle is quite obvious. Both pregnant and non-pregnant cycles were initiated in these quokkas by the removal of a pouch young, a stimulus sufficient to initiate the development of a dormant blastocyst if the quokka is pregnant as the result of a successful post-partum mating. A similar spike of progesterone has since been confirmed in the pregnant tammar by Hinds and Tyndale-Biscoe (1981) although a spike of lesser proportions is also evident in the non-pregnant cycle.

Circulating levels of progesterone in the maternal circulation are of course one of the crudest indices of the reproductive state of an animal and it is important to assess tissue reactivities to such hormones. Owen, et al. (1982) have recently characterized a high-affinity progesterone-binding receptor in the uterus of the quokka and monitored changes in this receptor throughout the oestrous cycle and pregnancy. Receptor
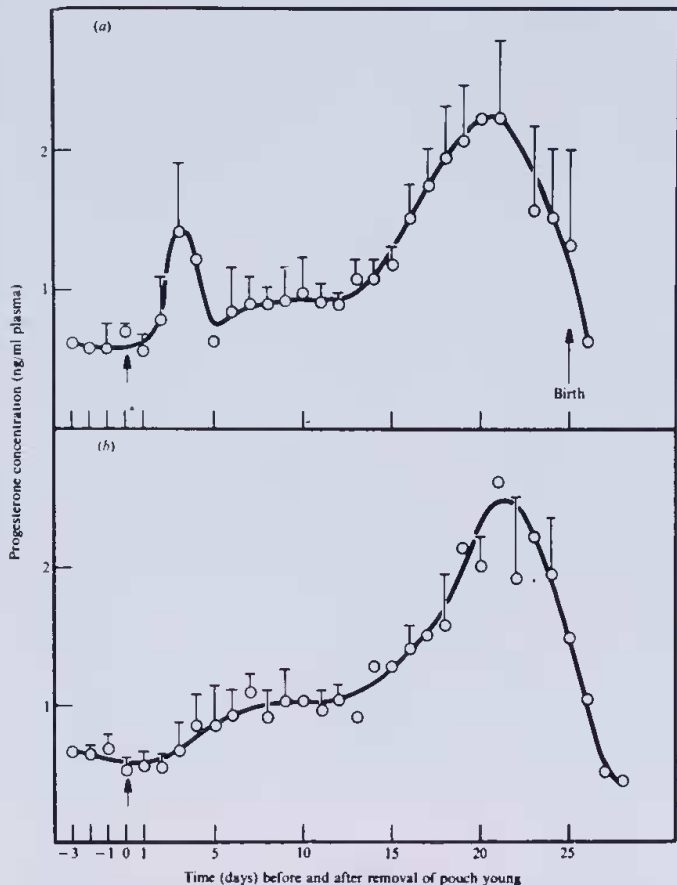
Figure 3.—Plasma progesterone concentrations in quokkas (*Setonix brachyurus*) following removal of a pouch young at time zero. A = pregnant cycle; B = non-pregnant (i.e. oestrous) cycle. The data are presented as Means ± S.E. of three individuals in each instance. (From Cake *et al.* 1980, with permission).

concentrations are always higher in the ipsilateral horn following ovluation than in the contralateral horn and this argues for a local circulation by which progesterone from the corpus luteum can differentially affect the adjacent uterus (see Lea and O'Shea 1977). There appears to be an effect of the blastocyst as receptor concentrations remain elevated in the pregnant horn on day 3 when compared with the non-pregnant horn (20.1 ± 5.9 pmoles/g wet weight versus 9.5 ± 2.1 pmoles/g wet weight, $p < 0.05$), whereas they are not different on day 3 in the oestrous cycle (Owen unpublished).

Conclusion

It is impressive to attest to the extent to which the quokka *(Setonix brachyurus)* has served as a vehicle for much of the research that has been carried out on the endocrinology of marsupials. Much of the early work on marsupial reproduction was done with the quokka and it has returned to prominence as a result of the recent progesterone studies. There is little doubt now that earlier conclusions as to the endocrine equivalence of the pregnant and oestrous cycles in marsupials were in error and recent studies have found differences, albeit subtle ones. Work on anterior pituitary hormones in marsupials is still in an early stage and sensitive homologous radio-immunoassays for the measurment of circulating levels of FSH and

LH have yet to be developed. The significance of Acher's discovery that the neurohypophysial hormones of marsupials (but not monotremes) are unique will only be clarified by further study. Similarly the metabolic effects of cortiocosteroids such as cortisol are obscure in species such as the quokka and future research on this interesting animal should prove highly rewarding.

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